Trade-offs

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Fast, cheap, good: pick two

Go into any programmers' cubicle farm and you are almost guaranteed to see some version of this diagram. Yes, yes, it's sort of funny, but more importantly, there's a deeper wisdom here. In short, when there is a limited resource—resources, energy, time—then you cannot have it all. You need to prioritize one thing at the cost of another[1].

Figure 1: Post-it note from any cube farm.

[1] Or, as the aphorism goes, "you aren't prioritizing if you aren't saying no."

It is worth noting that *something* is virtually always limiting, in all sorts of contexts. A public health department has a limited budget, a busy student has limited time (or attention), and a growing *Daphnia* has only so much energy and resources. It is worth noting that the limiting resource can be information, too! Remember that diagnostic tests could gain specificity at the cost of sensitivity, and vice versa. There is only so much information in a diagnostic test, and you so you bias it one way or the other.

It is also worth nothing that there are almost always competing interests. The public health department needs to educate health care workers, government officials, and the general public about health threats in hopes of preventing disease; test for a wide range of infectious and non-infectious diseases, collect data on current trends in disease incidence for numerous sources; and devise and implement responses to improve public health[2]. A *Daphnia* invests its limited energy and resources among growth, maintenance (e.g., anti predator defenses & behaviors, foraging, etc.), and reproduction[3].

[2] And this is the course-level of their duties!

[3] I assume you know the many competing interests of the time and attention of a busy student!

Optimal *Daphnia* and more

The question, then, is how to allocate these limited resources among the many competing interests or needs. The simple answer is that we should try to use them optimally. That is, we should allocate resources so as to maximize…something[4]. But there's the rub. What are we trying to maximize (or minimize)? It might seem straightforward, but I assure you, it is not.

A perfectly rational public health department might try to minimize human deaths in the population they serve, or maximize years of life or quality of life. They might realize that money and time spent on smoking prevention programs is much more effective than the same amount spent on smoking cessation programs, and both are more effective at maximizing quality years of life than, say, screening travelers for novel zoonotic pathogens that might, but probably will not, cause a global pandemic. Similarly, collecting data on which segments of a population

[4] Or many things. Indeed, this idea of optimality is a bit suspect because it overly simplifies the value or utility we try to maximize, the relationships between things we can change and those values, and the predictability of the whole thing. Moreover, sometimes being good enough is, well, good enough!

are likely to smoke (or vape[5]) can make for more targeted, effective anti-smoking campaigns, which might make that worth the extra effort. Or not. So in sum, a rational public health department might increase its smoking prevention programs at the cost of reducing its efforts to screen for less common or less important diseases. That is how they would navigate the trade-off.

When it comes to what the *Daphnia* are optimizing, things appear to be much simpler. Like all living organisms, *Daphnia* should maximize their fitness[6]. But what exactly does that mean? There are, literally, books written on what fitness is and how it can and should be measured. Let us use the common, but imperfect definition as the expected number of offspring (or grand-offspring) in the population. An optimal *Daphnia* should take whatever strategy maximizes the number of offspring it produces. This might, initially, suggest it should just pump out the clonal offspring, early and often! But, it is worth noting, that reproduction comes at the cost of growth—and larger individuals can produce more offspring per clutch—and maintenance, meaning there is a reduced chance of surviving to reproduce in the future. So reproduction now comes at the cost of future growth and reproduction.

There is no single optimum

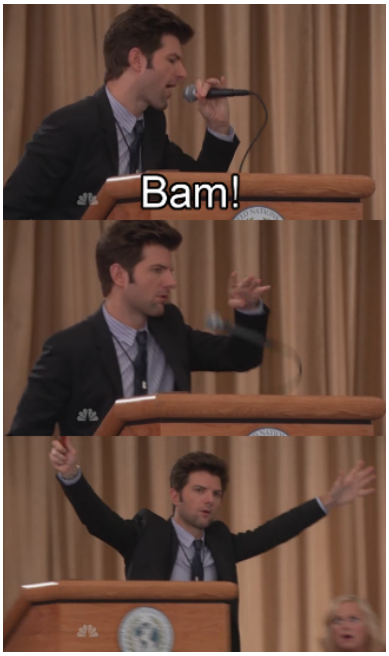
Before we get tied in knots thinking about what an optimal *Daphnia* (or any other critter) should do, it is worth noting two things. First, there are many winning strategies! Just look around you! You can probably see very long-lived trees that might take decades before the even begin to reproduce and very short-lived flies that live months and that might reproduce within a matter of days. Or think of you, in between the two. The tree might send out bazillions[7] of seeds every year, while even the most ambitious human female will have several dozen over a lifetime[8]. They and we and all sorts of other organisms have taken on all sorts of different strategies and the mere fact of their existence suggests that these strategies *work*!

Second, and relatedly, what is "optimal" depends on context. Are you liable to be eaten by a predator any day now? Well, reproducing sooner than later seems like a good plan. Can you expect to have more resources in the future to take good care of your young and thus ensure their survival? That seems like a good bet. In short, only when given something to maximize *and* a context can we perhaps predict what should be optimal.

Marginal value or diamond–water paradox

One of the key insights in many fields of study is that trade-offs between two things of value do *not* mean a simple one-to-one relationships or even a constant ratio (e.g., a dollar towards smoking prevention is worth five towards smoking cessation). Instead, the value of an investment depends on context (as we've just noted) and how much you already have of the thing(s) you might invest in.

[5] In the U.S. we tend to treat vaping as a gateway to smoking, whereas in the U.K. they think of vaping as a less-bad-for-you replacement for smoking. A lot of this comes from the public's perception of the morality of certain behaviors. It is hard to be a truly rational health department.



[6]

[7] Bigger than a handful, less than a googolplex.

[8] The record, according to Wikipedia is 69 children to a monogamous couple, although the numbers for male monarchs, religious leaders, and a weird collection of business men, polygamists, and sperm donors have eye-watering numbers!

Consider a classic economic paradox, called the paradox of value. Water is an essential resource for life, yes? But diamonds, which are not particularly useful outside of some industrial processes, are much, much more expensive! You can get a gallon of water for a dollar at the store or pennies from your tap at home. Indeed, you can get it for free at any drinking fountain. Diamonds, on the other hand, cost ridiculous amounts[9] Why is that?[10]

The simple version is that you have enough water already. If you were, say, dying of thirst you would probably pay a lot for that first gallon of water! You'd probably happily give up all your diamonds (or as the ridiculous advertisement say, "three months salary") for enough water not to die! I know I would! You'd probably even pay a lot for the second and third gallon. But by the 5th it might be less advantageous. You'd have to carry it or store it, which is inconvenient. By the 10th or 10000th you probably wouldn't pay much at all. That is to say, that the *marginal* value, the value of each extra gallon of water, starts out very high, but declines pretty quickly. Diamonds, on the other hand are worth about the same whether you have one or ten, if you're a diamond person; their marginal value declines much more slowly.

What does this mean for our trade-offs? Simply that a key part of what is optimal depends on how much you already have. If you are a health department who already invests a great deal in smoking prevention, investing even more may not get you much bang for your buck. Instead, investing in sex education, if you spend only paltry amounts currently, could lead to large gains. Similarly, a *Daphnia* that is already large might not gain much from investing in growth, but could instead devote those resources to maintenance or reproduction. Or one that is near the end of its life might not bother with maintenance or growth, because it is probably going to die soon no matter what it tries, but instead invest in reproduction, going out with a bang![11]

Once you start thinking about trade-offs, you see them everywhere. Here are a few examples:

[9] And lose much of their value as soon as you walk out of the store.

[10] I recommend this Planet Money story; it's far more entertaining that most accounts.

[11] No, *Daphnia* do not do that metaphorically or euphemistically.

Trade-offs in public health

Public health is the medical land of trade-offs. Not that individual medicine doesn't involve trade-offs (name brand or generic?), but when it comes to populations you are always pitting one group's interests against another's. There is no way those people get paid enough!

- One thing we heard a lot in this current COVID-19 pandemic is that the cure might worse than the disease. While this was often used to denigrate even basic public health interventions, there is an important point that should not get lost in the political back-and-forth. Keeping people home from schools and work has real costs. Kids get a *lot* out of being at school, from a better education to necessary social interactions to free lunches and other services. Keeping them home might reduce their risk of getting COVID-19, but it comes at a cost. Sometimes these costs clearly outweigh the benefits, though it can be difficult

to know[12].

- Recommendations for when and who to screen for various cancers (e.g., with mammograms, colonoscopies, etc.) often involve a trade-off between the costs—including the monetary costs, but also those of unnecessary worry, treatment, and surgeries that comes from false positives—and the costs of not finding these cancers early enough to intervene. Vaccines, too, involves trade-offs. There are side-effects and costs to vaccination. Are those costs outweighed by the reduced disease burden on the population?
- Chickens, pigs, and cattle are often culled to prevent the spread of disease between places or into humans. There is a clear economic cost to culling and often an uncertain benefit (would the disease really have spread?). This area is rife with trade-offs.

[12] I highly recommend this podcast on the costs of interventions, like closing trains down until all of the rails were checked for problems after a train crash or moving people out of the danger zone around the Fukushima Daiichi nuclear accident.

Trade-offs in life history

Evolution often, some would say *always*, deals with trade-offs. The perfect organism would start reproducing early, have huge numbers of offspring all the time, and live forever. Clearly that's impossible[13], so organisms that are the product of evolution trade-off one thing against another.

[13] But what about lobsters?

- Should an organism invest in adaptive immune system with immune memory and all of the other bells and whistles? Immune systems are expensive to build and maintain, and they keep trying to do stuff like attack one's own tissues if not carefully regulated. Plus, they take a long time to work, like weeks from initial infection to protective immunity. For a mouse that lives only 4–5 weeks on average, it's an open question whether having all of that stuff is actually worth the cost. I mean, how often can a mouse expect to be exposed to the same pathogen twice before it gets eaten or starves to death? Perhaps not often! The "Pace of life hypothesis" suggests that short-lived, fast-paced species—those with the rock star syndrome—probably should not invest much in maintenance and instead just pump out babies as soon as they can.
- A similar response can be seen when individuals are infected with pathogens that might kill or castrate them. *Daphnia*, for instance, infected with a castrating parasites reproduce earlier, even though it's a smaller brood, just to get some out while they can!
- You can see a similar pattern even in human populations. How do longevity or rates of early childhood mortality relate to family size? Pretty well!
- We can even see viruses and other parasites as facing trade-offs. If a virus replicates very fast it might attain a huge virus population, increasing the host's infectiousness, but that may comes at the cost of a shorter infectious period and thus fewer opportunities to get passed on. Indeed, this is called[14] the "trade-off hypothesis" for the evolution of parasite virulence. More on this slippery beast later.

[14] Do evolutionary ecologists like to name their hypotheses? Apparently…